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# The biotic crisis and the future of evolution

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**The biotic crisis overtaking our planet is likely to precipitate a major extinction of species. That much is well known. Not so well known but probably more significant in the long term is that the crisis will surely disrupt and deplete certain basic processes of evolution, with consequences likely to persist for millions of years. Distinctive features of future evolution could include a homogenization of biotas, a proliferation of opportunistic species, a pest-and-weed ecology, an outburst of speciation among taxa that prosper in human-dominated ecosystems, a decline of biodiversity, an end to the speciation of large vertebrates, the depletion of "evolutionary powerhouses" in the tropics, and unpredictable emergent novelties. Despite this likelihood, we have only a rudimentary understanding of how we are altering the evolutionary future. As a result of our ignorance, conservation policies fail to reflect long-term evolutionary aspects of biodiversity loss.**

**H**uman activities have brought the Earth to the brink of biotic crisis. Many biologists (e.g., refs. 1–5) consider that coming decades will see the loss of large numbers of species. Fewer scientists—witness the lack of professional papers addressing the issue—appear to have recognized that, in the longer term, these extinctions will alter not only biological diversity but also the evolutionary processes by which diversity is generated. Thus, current and predicted environmental perturbations form a double-edged sword that will slice into both the legacy and future of evolution.

A simple consideration of time underscores the magnitude of the challenge to scientists and public alike (*cf.* ref. 6). Episodes of mass extinction documented in the geological record were followed by protracted intervals of rediversification and ecological reorganization; five million years can be considered a broadly representative recovery time, although durations varied from one extinction to another (7). Suppose, too, that the average number of people on Earth during the recovery period is 2.5 billion (by contrast with the 6 billion today). Under these conditions, the total number of people affected by what we do (or do not do) during the next few decades will be in the order of 500 trillion—10,000 times more people than have existed until now. We are thus engaged in by far the largest "decision" ever taken by one human community on the unconsulted behalf of future societies.

The question of how current threats to biological diversity will affect the future of evolution was first raised by one of us in the mid-1980s (8). It attracted virtually zero interest from fellow biologists. Thirteen years later, he revisited the question, this time with more detailed analysis, although still in exploratory form (9). This latter publication elicited attention from the National Academy of Sciences, which undertook to sponsor a Colloquium in March 2000. As a "scene setter" for Colloquium participants, we drafted an overview account of topics to be tackled, and that draft makes up the bulk of this paper. We hope that it may serve the same purpose for readers of this special section of PNAS.

## The Core Concept

One of the first truisms absorbed by biologists is that evolution is not predictable. We can no more predict the future compo-

sition of communities than some Ordovician ecologist could have foreseen the Great Barrier Reef. However, despite our inability to predict the *products* of evolution—the trajectories of future morphologies or the innovations of future physiologies—we *can* make meaningful estimates about evolutionary *processes* as they will be affected by the depletion of biological diversity. We may have little basis for predicting what large mammals might look like two million years from now, but much better reason to suppose that there will be very few of them.

The evolutionary dimension to the current biotic crisis has been vividly expressed by Michael Soule (10): "Death is one thing, an end to birth is something else." In other words, impending extinctions will be far from the full final outcome of current environmental disruption. At least as important will be the alteration of evolutionary process, and for a period that is difficult to estimate but must surely measure in millions of years.

**First-Order Effects.** There will be several first-order effects stemming from the biotic crisis: (i) a major extinction of species within the foreseeable future, estimated by some to remove between one-third and two-thirds of all species now extant (1, 2, 5, 11); (ii) a mega-mass extinction of populations, proportionately greater than the mass extinction of species, within the foreseeable future (12); (iii) alien invasions and other mixings of biotas (13–16); (iv) progressive depletion and homogenization of biotas, with potential threshold effects on ecosystems (17, 18); (v) biotic impoverishment generally, possibly including a decline of global biomass (18–20); and (vi) gross reduction if not virtual elimination of entire sectors of some biomes, notably tropical forests, coral reefs, and wetlands, all of which have served as centers of diversification in the past (21–24).

**Further Evolutionary Effects.** These first-order impacts will likely engender a series of further consequences, including although not limited to: (i) fragmentation of species' ranges, with disruption of gene flow (25–28); (ii) decline in effective population sizes, with depletion of gene reservoirs/pools (12, 29, 30); and (iii) biotic interchanges introducing species and even biotas into new areas, with multiple founder effects and novel competitive and other ecological interactions (13, 16, 31). These impacts, in turn, might disrupt food chains/webs, symbioses, or other biological associations (32, 33).

These consequences could lead to further repercussions such as the following six:

**An outburst of speciation.** As large numbers of niches are vacated, in conjunction with a splitting off of disjunct populations through habitat fragmentation, there may well be an outburst of speciation, even of adaptive radiation, albeit not remotely on a scale to match the extinction spasm (34–36). It is unlikely that speciation will be evenly distributed among surviving lineages; it may be concentrated among particular clades or

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ecological types that thrive in human-dominated ecosystems (37, 38)?

**Proliferation of opportunistic species.** *r*-selected and generalist species, often appearing as opportunistic species, may proliferate, especially if there is preferential elimination of *K*-selected species that include natural controls of *r*-selected populations (32, 38). Could this proliferation lead to what has been characterized as a “pest and weed” ecology (39, 40)?

**Depletion of “evolutionary powerhouses” in the tropics.** Virtually every major group of vertebrates and many large categories of invertebrates and plants originated in spacious zones with warm, equable climates (41, 42). In addition, tropical species appear to have persisted for relatively brief periods of geologic time, implying high rates of evolutionary turnover and episodes of explosive speciation (21, 43, 44). According to Jablonski (22), the tropics have been “the engine of biodiversity” for at least 250 million years. Today, we face the prospect of severe depletion if not virtual elimination of tropical forests, wetlands, estuaries, coral reefs, and other biomes, with their exceptional biodiversity and ecological complexity. Because some of these biomes appear, in some senses at least, to have served in the past as preeminent “powerhouses” of evolution (45, 46), their decline could entail severe consequences for rediversification as the biosphere emerges from environmental crisis.

**Decline of biodisparity.** Elimination of species is not the only measure of an extinction event. There can be declines, as well, in biodisparity, the biota’s manifest morphological and physiological variety (47–49). Biodisparity impoverishment can be assessed through the surrogate measure of loss of higher taxa or guilds, and, over the past 2000 years, the preferential elimination of species-poor genera has reduced biodisparity at rates even greater than those of species loss (48). Will the same pattern of non-random culling persist in the future?

**An end to speciation of large vertebrates.** Even our largest protected areas will prove far too small for further speciation of elephants, rhinoceroses, apes, bears, and big cats, among other large vertebrates (30, 50, 51). What knock-on consequences and ripple effects could there be for smaller species, indeed for biotas as a whole given, for example, the depauperizing impacts of the present-day decline of elephants (52)?

**Emergent novelties.** There may be many emergent novelties, although these are especially difficult to predict. For instance, there could be an explosive radiation within certain higher taxa, notably small mammals and insects able to thrive in human-dominated ecosystems. The question is not whether persistent lineages can evolve in unexpected ways, but rather to what extent the environmental constraints humans place on surviving populations will channel innovations toward properties we associate with pests.

### Lessons from the Past?

The geological record is replete with extinction events, their intensity ranging from the small and local to global mass extinctions that shattered Earth’s biological order. Inevitably, extinctions were followed by rediversification, directed in the case of the largest events by ecological reorganization. What can we learn from paleobiology, other than the oft-quoted observation that recovery proceeds slowly in the wake of grand scale biotic disruption (40, 53, 54)? Can we find generalities among extinction episodes that can guide thinking about our own future? Or, is it the differences among extinction events that should command our attention? As David Jablonski (63) asks in these proceedings, should we even focus on the five great mass extinctions that capture most attention, or do the more numerous, smaller events scattered throughout the geological record provide closer analogs for the present?

The geologic record contains much evidence of bounce-back processes (49, 54–59), but how far will these serve as analytic

blueprints for what lies ahead? How can we estimate time frames at issue? Should we anticipate a minimum period of several million years [perhaps as much as 10 million (56)] before evolution can reestablish anywhere near the biological configurations and ecological circuitry existing before the current crisis? Will some recovery processes operate in some sectors of the biosphere, others in others, and with widely varying rates (55, 58, 60)?

In some major extinctions, for example the Cretaceous-Tertiary boundary event, environmental perturbation was swift and sure, but also short-lived. Recovery began soon after disruption. In the present biotic crisis, it is hard to envision a scenario under which the factors that are driving the biosphere toward grand scale biodiversity loss will be mitigated in the wake of such loss. On the contrary, on any time scale we can envisage (and any scenario that does not involve early mass mortality for humankind), the situation becomes bad and then stays bad for some time to come. Thus, on the time scale of the human species, environmental disruption (or at least aspects of it) is permanent. Under these circumstances (which may, to some degree, be approximated by the persistent environmental discord after the Permian-Triassic mass extinction), the prospects for rediversification are limited.

### Recovery Processes

How will ecosystems function in a world of diminished biodiversity? Does ecosystem function necessarily decay as diversity declines, and if so, by how much and in what manner? Can biodiversity and humans alike prosper in a world where most biological diversity will be confined to relatively small parks and reserves?

If biodiversity is indeed critical to ecosystem function, do we know enough about the principles of evolution to intervene in the recovery processes? To the extent that the answer to the first part of this question is probably “yes” and the answer to the second part is almost certainly “no,” what would we need to learn to attempt evolutionary interventions that will do more good than harm?

More realistically, do we know enough to mitigate the loss of biological diversity? As David Western writes in his colloquium contribution, mitigating strategies will likely be carried out predominantly in ecosystems dominated or influenced by humans and other species that thrive when humans are present. How we think about our evolutionary future depends directly on how successful we can hope to be in preserving biodiversity and biodisparity.

Which taxa are likely to play prominent parts in recovery processes? What “survivorship” traits (ecological, biogeographic, evolutionary) can we use to define those taxa that may prove more successful in surviving current events? At the same time, which taxa might [to cite Erwin’s graphic phrase (55)] “win the extinction but lose the recovery?” Might certain biotas already be “stressed” by Pleistocene climatic oscillations, making them more vulnerable to depletion (61, 62)? Or are they “hardened”—purged of their most vulnerable members by Pleistocene events (63)?

Should we in fact speak of “recovery”? What is it that is supposed to be recovering (the dinosaurs didn’t)? Should we not view the recovery phase as more like a transition to new and novel departures of multiple sorts (55)? Plainly there is much scope for pioneering research in response to the many questions raised (54). We need to consider planning priorities. What research is most pressing? What is readily achievable? What is already underway? What deserves most financial or institutional support? What potential is there for interdisciplinary research, for instance that which combines genetics and restoration ecology, or paleontology and conservation biology?

## Conservation Responses

Should we be content simply to safeguard as much as we can of the planetary stock of species? Or should we pay equal if not greater attention to safeguarding evolutionary processes at risk (cf. refs. 64–66)? Consider, for instance, biodiversity: to cite Jablonski (49), “If we are concerned with avoiding the loss of particular functional groups, or with maximizing the potential source pool for evolutionary recovery, then biodiversity measures may provide a more appropriate assessment, beyond sheer numbers of taxa, of how priorities should be set.”

Following on from these considerations is the question of whether we should seek to maintain the evolutionary status quo by preserving precise phenotypes of particular species, or whether we should prefer to maintain phylogenetic lines that will enable evolutionary adaptations to persist, thereby leading to new species (67, 68). Is it sufficient for us to maintain, for example, just the two elephant species we already have, or should we try to keep open the evolutionary option of further elephant-like species in the distant future?

This is an unusually significant question, with unusually significant implications for conservation strategies. Elephants, along with many other large mammals, are inclined to move around a good deal, a trait that enables them to maintain gene flow across large areas. As a result, their gene pools often tend to be fairly uniform [an elephant in East Africa may not be so different from one 4,000 km away in South Africa (68)]. Regrettably the remaining populations of elephants, substantial and extensive as they are, albeit fragmented and declining fast, are probably already below the minimum numbers to keep open the possibility of speciation (69).

In marked contrast to elephants, with their slow breeding rates, many insect species have immense breeding capacities and rapid turnover rates. These latter attributes offer quick adaptability to environmental shifts, whereupon genetic changes are passed along promptly. These attributes not only leave many insect species well suited to survive the environmental upheavals of human activities, but they offer exceptional scope for specia-

tion in comparatively short order. By contrast, elephants, together with other large-bodied species that reproduce slowly and hence possess restricted capacity for genetic adaptation, will be at an extreme evolutionary disadvantage. Does this factor imply that they should therefore receive all of the greater attention from conservationists—or that, in a triage situation, they should rank lower in our priorities? Although this is a fundamental question, it has hardly been addressed.

An even more important consideration arises concerning those origination centers and radiation lineages that serve as “evolutionary fronts” (67). From the standpoint of future evolution, it is surely more appropriate to safeguard the main potential for diversity generation than to emphasize the primary focus of many current conservation programs, viz. individual taxa and, especially, endemic taxa (70, 71). Much the same applies with respect to those functional groups that increase the potential for evolutionary recovery (49).

All in all, the prospect is that, in the wake of the present biodiversity crisis, we shall find that many evolutionary processes that have persisted throughout the Phanerozoic Eon will be slowed if not depauperized for an extended period. This is not to say, of course, that evolution will come to a halt, or even that speciation will be suspended (except for the large vertebrates). In fact, there may be enough creative disruption in certain environments to foster some extremely rapid microevolutionary changes, attended by (localized?) bursts of speciation. But there will surely be reduced scope for speciation on the scale that has characterized the past many millions of years.

These, then, are some of the issues that we should bear in mind as we begin to impose a fundamental shift on evolution’s course. We are “deciding” on evolution’s future in virtually a scientific vacuum—deciding all too unwittingly, but effectively and increasingly. Hence the importance of the Colloquium’s findings as set out in this special issue of PNAS.

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